

THREE SPECIES OF AUSTRALIAN MURICIDAE (GASTROPODA) WITH ANCESTORS IN THE AMERICAN TERTIARY

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Plates 1-3

SUMMARY

In three different genus-groups of Muricidae there is a close relationship between fossil species found in the Tertiary of the western Atlantic and modern forms living only off Australia. In two cases there are fossil Australian intermediate forms but in the third case the two species are unique. The species discussed are:

- (1) *Dermomurex* (*Viator*) *sexangulus*, *asteriscus*, and *antonius*;
- (2) *Murexiella* (*Subpterynotus*) *textilis*, *antedens*, and *tatei*; and
- (3) *Murex* (*Haustellum*) sp., and *wilsoni*.

INTRODUCTION

Continuing work on the western Atlantic species of the gastropod family Muricidae has revealed a number of unusual paleogeographic problems, including three different genus-groups in which close relationship occurs between American Tertiary forms and Australian Recent species.

DISCUSSION

The first example is that of a new Recent species of Australian *Dermomurex*, described in the accompanying paper as *D. (Viator) antonius* (see Pl. 1, fig. 1). This new species has a middle Miocene Australian ancestor in the form of "*Murex*" *asteriscus* Tate, 1888 (Pl. 1, fig. 3), from the Balcombian Muddy Creek Formation of Victoria. However, both these Australian species seem to be descended from the early Miocene (Aquitanian) *D. (Viator) sexangulus* (Dall, 1915) (Pl. 1, fig. 4) from the Atlantic Coastal Province of the United States. These three species are the only known members of this line, which apparently is derived from the *Dermomurex* (*Takia*) group still found living on the west coast of Mexico and in the Indo-Pacific.

The *Takia* line was widespread by the end of the Oligocene with species in the New World and in the Old, and it is probable that the Old World *D. (Takia) cotteavi* (Meunier, 1880) gave rise to the middle Miocene (Balcombian) *D. (Takia) pachystirus* (Tate, 1888), found in the Caddell Marl Member of the Morgan Limestone, Murray River, South Australia. This species in turn seemingly gave rise to the sole remaining Recent Indo-

Pacific member of the *Takia* line, *D. (Takia) infrons* Vokes [a new name, proposed in the accompanying paper, for "*Murex*" *inermis* Sowerby non Philippi]. It is possible that we have a case of parallelism with *D. cotteavi* giving rise to the *Viator* line in the Australian area, while independently in the New World the Oligocene species of *Takia* give rise to a markedly similar progeny in the form of *D. sexangulus*. Either way we must evoke a great deal of "remarkability" on one hand for the case for parallelism, or else for the case for transportation half-way around the world.

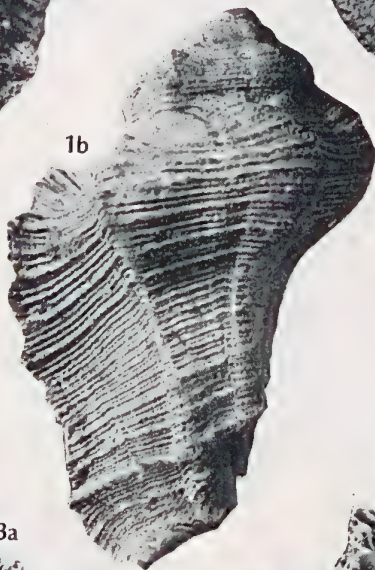
The fact that the United States member of the *Viator* line is found at a most unusual locality in terms of other species occurrences suggests that it is less difficult to accept the latter alternative. Silverdale, North Carolina, as I have discussed in another paper (Vokes, 1971a: 51) from whence comes the specimen of *D. sexangulus* here figured (Pl. 1, fig. 4), from all indications seems to have been in direct connection with a trans-Arctic route to the northern Pacific, as well as to Europe. Genera of Muricidae that are found at Silverdale in the Miocene are today living along the coast of the Pacific from Mexico and California to Japan (e.g., *Ocenebra*, *Ceratostoma*, *Purpurellus*) but are no longer in the western Atlantic.

There is a great deal that we do not know about long-distance movement of tropical shallow-water mollusks. We have no idea of the routes of migration nor even of the mechanism, for most stenoglossid gastropods do not have any pelagic larval stage (see Radwin and Chamberlin, 1973), and those that go through such a stage usually do not stay in this mobile state for more than about 10 days. How these animals manage to move across deep ocean basins is a mystery. One hesitates to evoke rafting on such a grand scale, and yet it seems to be the only logical solution. Either egg capsules or pregnant females (that is the only kind of animal that is ever rafted, it would seem from the literature) attached to floating driftwood could make the crossing, given a current in the right direction. Certainly modern gastropods are traveling on the bottoms of ships and doing strange things to distribution patterns. Undoubtedly new discoveries of intermediate species both in time and space, will be found in the future and perhaps some day we will have a better idea of Miocene migration routes from the tropical western Atlantic to southern Australia but as of now we must simply note the disjunct occurrences.

The generic assignment for the fossil species of *Viator*, both the American and the Australian ones, has been a problem to workers. Tate originally assigned his "*Murex*" *asteriscus* to the subgenus *Rhinocantha* [= *Bolinus*] (type species: *Murex brandaris* Linné). "*Murex*" *sexangulus* was referred to *Eupleura* (type species: *Ranella caudata* Say), an even less likely choice. When I described the species from North Carolina as new, not recognizing the previously described *M. sexangulus* as being the same, I referred the form to the subgenus *Panamurex* (type species: *Murex gatunensis* Brown and Pilsbry). It was not until the discovery of a living example of the group, the new Australian species described in the com-

PLATE 2

1. *Murexiella (Subpterynotus) antecedens* (Ludbrook, 1958). Tennant's Bore, Salisbury, South Australia. Holotype, X 2. SAM-Tate Coll. F 15198.
2. *Murexiella (Subpterynotus) tatei* (Verco, 1895). Smoky Bay, South Australia, 37 m. Figured specimen, X 3. Wright Collection, Sanibel, Florida. M-623.
3. *Murexiella (Subpterynotus) textilis* (Gabb, 1873). Unknown locality, Dominican Republic. Holotype, X 3. ANSP 3257.



panion paper, that finally the affiliation with the aspelloids was made apparent. Armed with this knowledge a close examination of specimens of "*Murex*" *sexangulus* revealed traces of the characteristic intritacalx. Comparison of Plate 1, fig. 1, with figs. 2 and 3 gives some indication of what the species probably looked like in life.

A problem in generic assignment is also present in the second set of species, the American representative being the unusually beautiful *Murexiella textilis* (Gabb, 1873), type of the subgenus *Subpterynotus* (see Pl. 2, fig. 3). This species first occurs in the late lower Miocene (Burdigalian) Chipola Formation of Florida and continues through the late Pliocene Caloosahatchee Formation of the same area. In the Burdigalian of Italy there is another nominal species *Murexiella granifera* (Michelotti, 1841), well figured by Bellardi (1873, pl. 5, fig. 1), that is so close to the American form it may well be the same species. Here at least we have a suggestion of a trans-European route. Very probably the line originated in the southern European region, as there are several related forms in that general area, and migrated east to Australia and west to the Caribbean (it occurs from Florida to Venezuela).

The genus *Murexiella* is one of the original muricid forms, being present in the Eocene of both the Old World and the New. The present stock has continued through time with virtually no change and there are several living species that differ little from the Eocene ancestors. In the Miocene of Europe we see the subsequent development of two divergent stocks, one of which gave rise to the modern species assigned to the genus *Homalocantha* (type species: *Murex scorpio* Linné). There are several Mio-Pliocene species in southern Europe that are clearly of this latter group. If it were not for the known anatomical differences of the living species of *Homalocantha* it is probable that the fossil forms would be placed with typical *Murexiella*. But the living members of *Homalocantha* are a problem in a subfamilial placement. Because of the obvious *Murexiella* ancestry I have placed the genus in the subfamily Muricopsinae in spite of the atypical radula, which would indicate placement in the Muricinae, and the atypical operculum, which would place the genus in the Ocenebrinae. *Homalocantha* is a genuinely intermediate genus.

Both *Murexiella* and *Homalocantha* are characterized by having usually five to seven varices. The members of the second branch, *Subpterynotus*, begin life with numerous varices but on the fifth post-nuclear whorl these are reduced to only three per whorl with three large intervarical nodes replacing the missing varices. Because nothing was known of the animal *Subpterynotus* was left with *Murexiella*, although the similarities to the fossil members of *Homalocantha* are very marked. However, recently a living species was recognized when two examples of "*Murex*" *tatei* Verco,

PLATE 3

1. *Murex (Haustellum) wilsoni* (D'Attilio and Old, 1971). Off Carnarvon, Western Australia, 146 m. (dead). Figured specimen, X 1½. Vokes Collection. Tulane University.
2. *Murex (Haustellum)* sp. Las Calderas. Island of Cubangua, Venezuela. Figured specimen, X 1½. UCPD 14142.

Abbreviations for various museums:

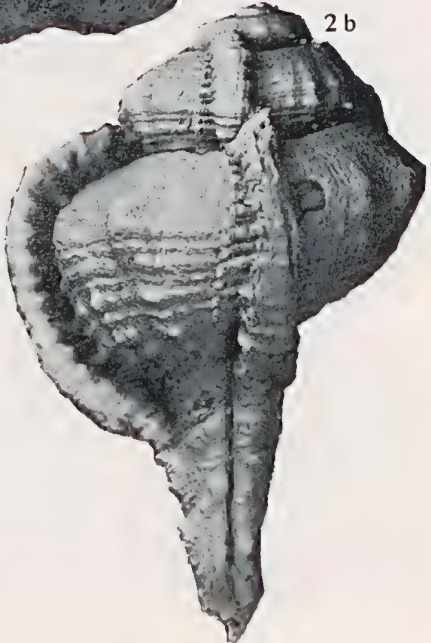
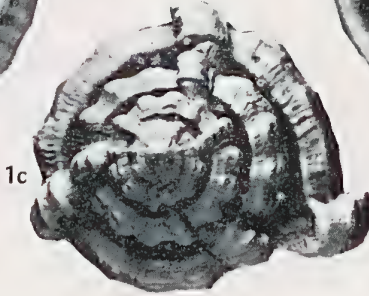
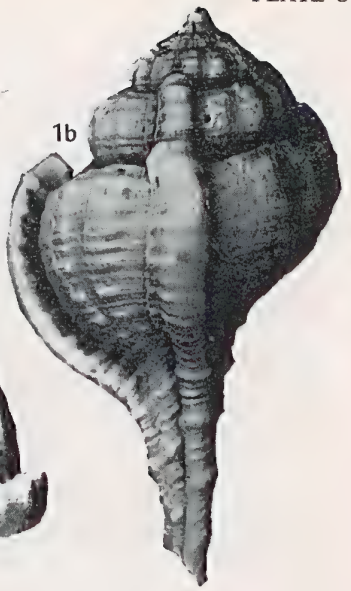
ANSP — Academy of Natural Sciences of Philadelphia, Pennsylvania.

SAM — South Australian Museum, Adelaide, South Australia.

UCPD — University of California, Museum of Paleontology, Berkeley, California.

USNM — United States National Museum, Washington, D.C.

WAM — Western Australian Museum, Perth, Western Australia.



1895, were dredged off Smoky Bay, South Australia, by Mr and Mrs. D. C. Pearsons. On the basis of the rather poor original illustration I had assumed "*Murex*" *tatei* was a *Murexiella* s.s. but when I saw the good specimens, one of which is figured here (Pl. 2, fig. 2), the *Subpterynotus* affinities were too obvious to ignore, in spite of the fact that *M. tatei* has more than three varices. This same conclusion had been reached independently at approximately the same time, by Ponder (1972: 230).

Murexiella tatei has a normal muricine operculum, suggesting that the designation of *Murexiella* subgenus *Subpterynotus* is valid, rather than a possible *Homalocantha* subgenus *Subterynotus*. The reasons for placing *tatei* with *Subpterynotus* rather than with *Murexiella* s.s. is the nature of the ornamentation. *Murexiella* s.s., and the same is true for *Homalocantha*, always has distinct "digitations" on the varices, with a fine webbing connecting them. *Subpterynotus* does not have the digitations but has a flanged varix with the tips of the grooves on the varical faces not noticeably longer than the webbing. In the members of *Homalocantha*, in addition to these digitations, there is often a peculiar "pad" or flattened spot in the anal region, which is well developed in *H. secunda* (Lamarck), the true Australian representative of *Homalocantha*.

It should be noted in passing that Ponder (*loc. cit.* p. 231) has made *Murexiella* a subgenus of *Favartia* Jousseume, 1880. On the surface there is no objection to this assignment for the two forms certainly intergrade into one another. However, this results in the necessary designation of *Favartia* subgenus *Subpterynotus*. All generic placements are subjective but to me the latter is untenable. This is a recurring problem in taxonomy, the Law of Priority as applied to generic and subgeneric rankings. If it were possible to designate the oldest geologic form or the central morphologic type as the genus regardless of nomenclatorial priority then these taxa could be given the more acceptable assignment of *Murexiella* (*Favartia*) and *Murexiella* (*Subpterynotus*). Unfortunately this is not the case, so I prefer to see the two recognized as separate genera.

In addition to the American-Italian Miocene ancestor and the Recent Australian descendant there is another species that clearly is of this group, as was also noted by Ponder (*loc. cit.*, p. 230), and that is the Pliocene Australian "*Homalocantha*" *antecedens* Ludbrook, 1958 (*Trans. R. Soc. S. Aust.*, 81: 58). This latter species, the holotype of which is figured here (Pl. 2, fig. 1), differs from its modern counterpart chiefly in size. *M. (Subpterynotus) antecedens* is some 40 mm in height but *M. (S.) tatei* is only about 25 mm. *M. (S.) texilis* is also a larger species with Pliocene American individuals attaining an average size of 50 mm.

In addition to *Murexiella tatei* there is a second living species of *Subpterynotus*. This is *M. (S.) exquisita* (Sowerby, 1904) described without locality and not recognized since. This latter species, although obviously belonging to *Subpterynotus*, is not extremely close to the species under discussion here, but seems to be a separate line of descent from the French Burdigalian species *M. (S.) subgranifera* (Cossmann and Peyrot, 1923). Both of these latter species are characterized by a marked shoulder angulation, which together with the reduced flange on the siphonal canal gives the shell a distinctly triangular aspect.

The third instance is the strangest perhaps, as there are no other species that even bear a remote resemblance to either of this pair. If the

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remarkable similarity between them is due solely to convergence it is an incredible happenchance. The American member of the pair has not been named as it is represented by a single shell in the collections of the Museum of Paleontology of the University of California, Berkeley. In this specimen the varices are deeply excavated abaperturally and the suture is marked by a strange deep channel otherwise seen in only one other muricine species. That is the Australian *Murex (Haustellum) wilsoni* (D'Attilio and Old, 1971). Comparison of the specimens of *M. wilsoni* and *M. sp.* (Pl. 3, figs. 1 & 2) clearly shows the several points of similarity between the two forms. *M. wilsoni* has other more distant relatives in the few species of *Haustellum* found in the Indo-Pacific area, especially in the Australian *M. (Haustellum) tweedianus* Macpherson, 1962. Only one species of *Haustellum* shows a tendency towards the sutural channel seen in these two strange forms and that is the Japanese *M. longicaudus* Baker (*M. kurodai* Shikama, 1964, is the same species), a form otherwise very much like *M. haustellum* Linné, type of the subgenus.

The generic distinctiveness of *Haustellum* has been based upon the constricted anal notch and the atypical operculum with its central nucleus. However, except in the type species and those very close to it (*M. longicaudus* and *M. fallax*) the anal notch is greatly reduced and the peculiar operculum is also found only in these species. The other Australian *Haustellum*, *M. tweedianus* shows a slight anal notch but has a normal muricine operculum. Inasmuch as the operculum with a central nucleus also occurs sporadically in other muricine species (e.g., *Murex pecten* Lightfoot), it probably is not a strict subgeneric character. The nature of the operculum in *M. wilsoni*, unfortunately, is not known.

Does the failure of these so-called generic criteria to hold up, therefore, mean that *Haustellum* should be abandoned? I do not think so. There is a distinct morphotype for which this name is useful, and this is the almost totally spineless form of three-varixed *Murex*. D'Attilio and Old (1971: 317) suggested the use of *Tubicauda* Jousseau, 1880, for these "atypical" species of *Haustellum*, including *M. tweedianus*, but the type species of that taxon, *M. brevispina* Lamarck, 1822, has very definite, although short, spines and cannot logically be segregated from *Murex s.s.* When one examines any group of species there are certain ones that can be unquestioningly assigned to the subgenus; in this category we would include *M. wilsoni* and *M. tweedianus* (in addition to the obvious *Haustellum haustellum*-like forms). There will also be intermediate species that could be placed with equal facility in either of two (or sometimes more) subgenera; this would include *M. multiplicatus* Sowerby, 1895, and *M. hirasei* Dautzenberg in Hirase, 1915. These latter species have been included in *Haustellum* by me in previous works (1964; 1971b) but they could just as well be placed in *Murex s.s.* This is a basic flaw in trying to divide a natural continuum of species into distinct "quanta."

The geologic history of *Haustellum* is almost totally unknown. It seems to have always been an Indo-Pacific group. There is nothing in the New World either in the fossil record or in the Recent fauna that bears any resemblance to the line. *M. wilsoni* can be derived from the typical *Haustellum* with no difficulty, and so it seems inescapable that in this case the origins of the American species lie in the southern Pacific area. How one single specimen found its way to the Island of Cubagua, Venezuela, to be deposited in the Pliocene Cumaná Formation, without leaving any

trace of its passage is another mystery. There is no question about the authenticity of the Cubagua specimen, as the characteristic yellow color marks its point of origin. A search for other specimens in the collections of the various Venezuelan institutions was conducted by Mr. J. Gibson-Smith, of Caracas, and he reported no success.

It is unfortunate that the sole specimen of the American species is badly worn and the early whorls are missing. If it should prove to have the unusual mammilated protoconch of the Australian species *M. wisoni*, then any possible chance of convergence certainly would be ruled out.

Thus we see three completely different genus-groups, each of which shows almost undeniable evidence of some sort of inter-continental migration that cannot be explained in the light of our present knowledge. There are undoubtedly many other instances just as striking, these are the ones which have come to my attention. It is hoped that time will bring additional information and the discovery of new fossil species may point the way to a better understanding of the routes and mechanisms of these migrations. But at the present time all that can be done is to call attention to the problem.

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